

Water sources used by riparian trees varies among stream types
on the San Pedro River, Arizona

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Abstract

Variation in the sources of water used by trees species has important ramifications for forest water balances. The fraction of tree transpiration water derived from the unsaturated soil zone and groundwater in a riparian forest was quantified for *Populus fremontii*, *Salix gooddingii*, and *Prosopis velutina* across a gradient of groundwater depth and stream flow regime on the San Pedro River in southeastern Arizona, U.S.A. The proportion of tree transpiration derived from different potential sources was determined using oxygen ($\delta^{18}\text{O}$) and hydrogen (δD) stable isotope analysis in conjunction with 2- and 3-compartment linear mixing models. Comparisons of $\delta^{18}\text{O}$ and δD of tree xylem water with that of potential water sources indicated that *Salix gooddingii* did not take up water in the upper soil layers during the summer rainy period, but instead used only groundwater, even at an ephemeral stream site where depth to groundwater exceeded 4 m. *Populus fremontii*, a dominant ‘phreatophyte’ in these semi-arid riparian ecosystems, also used mainly groundwater, but at the ephemeral stream site during the summer rainy season this species derived between 26 and 33 % of its transpiration water from upper soil layers. Similarly, at the ephemeral stream site during the summer rainy period, *Prosopis velutina* derived a greater fraction of its transpiration water from upper soil layers, than at a perennial stream site where groundwater depth was less than 2 m. Measurements of transpiration flux combined with stable isotope data revealed that *Populus fremontii* transpired a greater *quantity* of water from upper soil layers at the ephemeral than at the perennial stream site. These results imply that transpiration from groundwater and unsaturated soil layers by riparian vegetation may depend on the interaction between site conditions and species assemblage.

1 **Key words:** $\delta^{18}\text{O}$, δD , plant water sources, cottonwood, willow, mesquite, *Salix*
2 *gooddingii*, *Populus fremontii*, *Prosopis velutina*, leaf water potential, phreatophytes

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1. Introduction

Riparian forests in the southwestern United States are characterized by a mixed assemblage of obligate phreatophytes (plants that send their roots into or below the capillary fringe to use groundwater) and facultative phreatophytes (plants that can also survive in upland environments where groundwater is not available). However, extreme spatial and temporal dynamics of water within riparian ecosystems in arid and semi-arid regions can place severe constraints on the ability of trees to meet transpiration requirements during key periods of the growing season. For example, groundwater pumping and surface water diversions have produced dramatic changes in stand structure and species composition of riparian areas in this region (Stromberg and Patten 1990). Successful conservation of these forests will require knowledge on the dependence of riparian species on groundwater and conversely, on the feedback between riparian vegetation and stream and groundwater dynamics. Not all woody species in these forests use only groundwater for transpiration as the term 'phreatophyte' implies. Use of growing season precipitation can vary considerably among different woody species in the riparian environment (Smith et al. 1991, Busch et al. 1992, Thorburn and Walker 1994, Kolb et al. 1997). However, many widely used hydrologic models assume that riparian trees derive water principally from the saturated zone (McDonald and Harbaugh 1988), which is clearly an oversimplification. Characterization of the conditions that promote use of alternative water sources and identification of those species most likely to use these water sources in riparian forests is necessary to accurately assess water budgets at the catchment level in semi-arid and arid basins.

1 The long-term reliability of groundwater may encourage riparian trees to develop
2 roots predominantly in the capillary fringe and saturated zone rather than throughout the
3 soil profile, especially if precipitation during the growing season is unreliable (Ehleringer
4 and Dawson 1992). Conversely, plants that maintain roots in many soil layers, or that
5 can rapidly deploy roots into moisture-rich patches in the soil, may respond
6 opportunistically to precipitation. Research on riparian trees using stable isotope analysis
7 has provided evidence for both modes of root system function. In Australia, *Eucalyptus*
8 spp. used various combinations of groundwater, rainfall-derived shallow soil water, and
9 stream water (Mensforth *et al.*, 1994, Thorburn and Walker 1994, Dawson and Pate 1996,
10 Jolly and Walker 1996). Trees along a perennial, montane stream in California took up
11 water from upper soil layers early in the growing season, then used primarily
12 groundwater when soil dried (Smith *et al.* 1991). In western Arizona, *Populus fremontii*
13 and *Salix gooddingii* used groundwater throughout the entire growing season at perennial
14 and ephemeral streams, regardless of depth to groundwater (Busch *et al.* 1992).
15 However, responses of these trees to precipitation events were not assessed in this
16 Mojave Desert environment. Similarly, mature *Acer negundo* trees in northern Utah used
17 only groundwater, and did not appear to use perennial stream water or shallow soil water
18 (Dawson and Ehleringer 1991). In contrast, this species did use soil water from
19 precipitation at ephemeral and perennial stream reaches in Arizona (Kolb *et al.* 1997).

20 Although previous studies addressed various components of riparian ecosystems
21 and tree water sources, questions still remain about the integrated effects of groundwater
22 depth and flow regime on the ability of riparian trees to take up precipitation during the
23 growing season. Knowledge of species-specific responses to growing season

1 precipitation and constraints on deep and shallow root function for water uptake will
2 facilitate predictions of how habitat variation and declining groundwater affect patterns
3 of transpiration in riparian ecosystems.

4 The upland species *Quercus gambelii*, *Juniperus osteosperma*, and *Pinus edulis* in
5 the southwestern United States derived greater proportions of their transpiration water
6 from summer precipitation as the amount of these rains increased across a broad climatic
7 gradient (Williams and Ehleringer, *in press*). Intraspecific variation of this type implies
8 that the distribution of functional roots in woody species varies significantly across
9 resource supply gradients. However, the tradeoffs associated with this variation have not
10 been addressed. For instance, it is not known if development of roots in one zone of the
11 rhizosphere comes at the expense of root activity elsewhere. Additionally, plants with
12 roots deployed in upper soil layers should experience a greater amplitude of soil water
13 availability compared to plants that access a deep, stable water source. Plant predawn
14 water potential (Ψ_{pd}), therefore, should be correlated with plant water sources (Dawson
15 and Ehleringer 1998). A better understanding of the tradeoffs between plant water
16 balance and active rooting depth will help resolve linkages between groundwater, soil
17 water, and transpiration in riparian forests.

18 The riparian forest sites addressed in the current study receive a high proportion
19 (approximately 60%) of annual precipitation from summer ‘monsoon’ storms. Thus it
20 was predicted that at least some of the dominant riparian trees would use summer
21 precipitation. As in most riparian environment in semi-arid regions, the floodplains
22 varied in depth to groundwater that may further differentiate shallow soil water use
23 among the dominant riparian species. This study addressed seasonal patterns of water

source use by dominant riparian tree species at sites with contrasting groundwater depths and stream flow conditions. This study was part of the Semi-Arid Land Surface Atmosphere (SALSA) Program (USDA-ARS, Tucson, AZ) whose primary aim was to validate models for basin-wide water balances (Goodrich *et al. this issue*). The specific objectives of this study were to: (1) determine if riparian tree species along the San Pedro River in southeastern Arizona use growing season precipitation; (2) assess whether depth to groundwater influences the capacity for these trees to use precipitation; and (3) characterize physiological consequences associated with specific rooting patterns.

2. Methods

Study sites

Three sites were selected to represent a gradient in stream flow and groundwater availability. All sites were located within the San Pedro National Riparian Conservation Area at elevations between 1150 and 1250 m (ca. 31° 33' N; 110° 07' W). The San Pedro River is a low-gradient alluvial drainage that flows from Sonora, Mexico north to the Gila River in southern Arizona. Mean precipitation at the three sites is 330 mm per year, with 60% of the rain falling in the summer and most of the remainder falling in winter months (NOAA 1996). The hydrologic regime at the three sites was perennial (Lewis Springs), intermittent (Boquillas Ranch), and ephemeral (Escapule Wash). The riparian floodplain vegetation consisted of *Populus fremontii* (Fremont cottonwood) and *Salix gooddingii* (Goodding willow) as the dominant and sub-dominant overstory species. In this region these species, both classified as obligate phreatophytes, generally form a narrow gallery forest in active floodplains (Stromberg 1993). *Prosopis velutina* (Velvet

mesquite) was present as a sub-dominant tree and as an understory shrub within the *Populus/Salix* gallery forests. *Prosopis velutina* is a facultative phreatophyte that also occurs in xeric upland sites where groundwater is unavailable. Hereafter, these taxa will be referred to as *Populus*, *Salix*, and *Prosopis*.

Sampling Methods

Between five and eleven tree clusters with each of the three species present were randomly selected at each site. Clusters were not considered blocks in a statistical sense because species were analyzed separately. Trees were sampled in spring (April 19-24), summer (June 7-11, July 9-11, August 8-11) and fall (September 20-27) in 1997. April sampling occurred after *Populus* experienced spring leaf-flush. June and July sampling periods coincided with the annual dry season for this region. Sampling in August was performed during the height of the growing season and after a large monsoon precipitation event which did not produce over-bank flooding. During this single precipitation event, 27 mm of rainfall was measured at the perennial stream site, which fell during a single hour; trees were sampled 7, 8, and 10 days after the rainfall event at the ephemeral, intermittent and perennial stream sites, respectively. September sampling followed a series of storms that produced over-bank flooding along the perennial reach at the end of the growing season.

Stable isotopes of oxygen in xylem water extracted from twigs were used as natural tracers for determining the fraction of water taken from groundwater and unsaturated soil layers (Ehleringer and Dawson 1992, Brunel *et al.* 1995). Plant stems of approximately 0.5 cm in diameter were sampled at midday from sunlit branches and

1 stored in airtight glass vials for subsequent analysis of hydrogen and oxygen isotope
2 ratios (δD and $\delta^{18}O$). Soils were collected at each site from 5-, 10-, 25-, 50-, and 100-cm
3 depths for analysis of δD and $\delta^{18}O$ of water and gravimetric water content (θ_g). Local
4 floodplain groundwater was collected from wells at each sampling period and at all sites.
5 At the perennial reach, regional groundwater was collected from a deep (11 m) well
6 located approximately 300 m from the stream and outside the local floodplain.
7 Precipitation was collected at all sites in standard rain gauges that contained a layer of
8 mineral oil to minimize evaporation. These integrated precipitation samples were
9 collected monthly throughout 1997. A Scholander-type pressure chamber (PMS,
10 Corvallis, OR) was used to measure predawn leaf water potentials (Ψ_{pd}) on every
11 sampling date.

12 Stable Isotope Analysis

14 Water was extracted from plant stems and soils by cryogenic vacuum distillation
15 (Ehleringer and Osmond 1989). Plant, soil, stream, and groundwater samples were
16 analyzed for oxygen isotope ratios ($\delta^{18}O$) on a Finnigan Delta-S isotope ratio mass
17 spectrometer using CO_2 equilibration (University of Arizona Geosciences Stable Isotope
18 Facility). A subset of samples was also analyzed for hydrogen isotope ratios (δD) using a
19 chromium reduction furnace (HD-Device, Finnigan-Mat, Bremen, Germany) to convert
20 liquid water to hydrogen gas.

1 Data analysis

2 Plant $\delta^{18}\text{O}$ values were compared with those of soil water from different depths
3 and groundwater to determine sources of plant transpiration water. One-sided t-tests ($\alpha =$
4 0.05) were used to determine if mean $\delta^{18}\text{O}$ of a species at a given site was more positive
5 (enriched) than $\delta^{18}\text{O}$ of floodplain groundwater in June, July and August. Normality of
6 $\delta^{18}\text{O}$ data was determined with the Shapiro-Wilk test. δD - $\delta^{18}\text{O}$ relationships of isotopic
7 values from 10-, 25- and 100-cm soil depths, extracted plant water, rainfall and
8 groundwater were used to determine further differences in plant water source use (Craig
9 1961, Clark and Fritz 1998). Source waters with similar $\delta^{18}\text{O}$ or δD values may have
10 different δD - $\delta^{18}\text{O}$ relationships due to evaporation conditions.

11 Although $\delta^{18}\text{O}$ and Ψ_{pd} values are presented for all sampling periods, statistical
12 analyses were restricted to June, July and August. This restriction was due to
13 phenological differences among species (*Prosopis* and *Salix* were not fully leafed out in
14 April), and because, large storms produced over-bank flooding at the perennial site in
15 September. Over-bank flooding percolated through the soil creating similar $\delta^{18}\text{O}$ values
16 to a depth greater than 1 m. Therefore, it was not possible to distinguish use of monsoon
17 precipitation from groundwater and floodwater use. Multivariate analysis of variance
18 (MANOVA; $\alpha = 0.05$) was used to analyze the effect of site and sampling date (June,
19 July and August) on the difference between plant $\delta^{18}\text{O}$ and groundwater $\delta^{18}\text{O}$ for each
20 species (Von Ende 1993). This difference was used to standardize plant response across
21 sites even when there were shifts in local groundwater $\delta^{18}\text{O}$ values. ANOVA models (α
22 = 0.05) were used to compare sites within years if MANOVA revealed a significant
23 interactive effect. Since it was expected that sampling date would produce an effect on

1 $\delta^{18}\text{O}$, differences within a site across dates were not analyzed. Contrasts ($\alpha = 0.05$) were
2 used to determine differences between sites. Plots of residuals indicated that calculated
3 $\delta^{18}\text{O}$ differences were linear and normally distributed with homogenous error variances,
4 thus meeting the assumptions of MANOVA.

5 In cases where plant $\delta^{18}\text{O}$ differed significantly from that of local groundwater,
6 the fraction (f) of total plant xylem water derived from shallow soil layers (0-50 cm) was
7 calculated using a 2-compartment linear mixing equation of the form:

8
9 [Eqn. 1]
$$\delta^{18}\text{O}_t = f(\delta^{18}\text{O}_s) + (1-f)(\delta^{18}\text{O}_{\text{gw}})$$

10
11 where $\delta^{18}\text{O}_t$ was the measured $\delta^{18}\text{O}$ of tree xylem sap, $\delta^{18}\text{O}_s$ was a weighted average of
12 the measured $\delta^{18}\text{O}$ values of soils sampled at 5-, 10-, 25-, and 50-cm depths. Soil $\delta^{18}\text{O}$
13 values were weighted by gravimetric water content (θ_g) at each depth by dividing mean
14 θ_g at each depth by the sum of θ_g at all depths. $\delta^{18}\text{O}_{\text{gw}}$ was the measured $\delta^{18}\text{O}$ value of
15 groundwater. The equation was solved for f , the fraction of total plant water obtained
16 from water in shallow soil layers. Differences between sites were determined for each
17 species using t-tests.

18 At the intermittent stream site, the use of a 2-compartment model was
19 inappropriate because of the existence of a third source of plant water. Therefore a 3-
20 compartment linear mixing model was used. This was done using plant and source $\delta^{18}\text{O}$
21 and δD to produce two equations for tree water source. These two equations, in
22 combination with a third equation (for constraining the sum of the source fractions to
23 one) produced a system of three equations and three unknown variables of the form:

1

2 [Eqn. 2] $\delta^{18}\text{O}_t = a(\delta^{18}\text{O}_{S1}) + b(\delta^{18}\text{O}_{S2}) + c(\delta^{18}\text{O}_{S3})$

3 [Eqn. 3] $\delta\text{D}_t = a(\delta\text{D}_{S1}) + b(\delta\text{D}_{S2}) + c(\delta\text{D}_{S3})$

4 [Eqn. 4] $1 = a + b + c$

5

6 where $\delta^{18}\text{O}_t$ and δD_t are the oxygen and deuterium values of extracted plant water. The
7 subscripts S1, S2, S3 are sources 1, 2, and 3, respectively. a, b, c are the fractions of total
8 plant xylem water derived from sources 1, 2, and 3. Equations were solved
9 simultaneously using algebraic substitution. Results were checked using MatLab
10 (MathWorks, Inc., Natwick, MA).

11 To analyze effects of site and date (June, July, August) on Ψ_{pd} , MANOVA,
12 ANOVA and contrasts were used as described above. Data were transformed as
13 necessary to meet the assumptions of MANOVA based on inspection of residual plots.
14 Non-transformed values are presented in the figures and text. For each species within a
15 site, linear regression analysis was used to quantify the relationship between Ψ_{pd} and
16 $\delta^{18}\text{O}$ measured throughout the growing season.

17

18 **3. Results**

19 Mean depth to groundwater was 1.80, 2.67 and 4.26 m at the perennial,
20 intermittent, and ephemeral stream sites, respectively (Table 1). Median stream flow
21 along the perennial reach of the San Pedro River measured downstream of our study site
22 at the Charleston gauge for the period January 1997 to October 1997 was $0.2 \text{ m}^3 \text{ s}^{-1}$.
23 (Tayadon *et al.* 1998). Stream flow was observed along the intermittent reach for 11

1 months of 1997, but there was no flow in July. Flow occurred only briefly during storm
2 events at the ephemeral stream site. Stream flow was observed twice in August at this
3 site, but may have occurred during other storms as well.

4 Monsoon rains had $\delta^{18}\text{O}$ values ranging from 2.0 to -3.5 (‰) (Fig. 1), while
5 winter precipitation had more negative $\delta^{18}\text{O}$ values ranging from -4.4 ‰ to -8.7 ‰ (data
6 not shown). $\delta^{18}\text{O}$ values of groundwater sampled from the local floodplain did not vary
7 much over the growing season at the perennial and ephemeral reach, averaging -8.3 ± 0.2
8 ‰ (± 1 SE) and -8.4 ± 0.2 ‰, respectively (Fig. 1). In late September, after a
9 particularly large series of storms, groundwater at the ephemeral reach was enriched
10 (more positive) ($\delta^{18}\text{O} = -7.8$ ‰) relative to previous sampling periods. $\delta^{18}\text{O}$ of local
11 floodplain groundwater at the intermittent stream site varied substantially (Fig. 1).
12 During April, June, and July, the local floodplain groundwater ($\delta^{18}\text{O} = -7.3 \pm 0.15$ ‰)
13 isotopically resembled $\delta^{18}\text{O}$ of winter precipitation (-6.1 ± 0.35 ‰) at the intermittent
14 stream site. However, during the summer rainy season in response to storm and flow
15 events, $\delta^{18}\text{O}$ of local floodplain groundwater at this site was substantially enriched ($-4.9 \pm$
16 0.07 ‰) and reflected $\delta^{18}\text{O}$ of monsoon precipitation and recent stream flow. Isotopic
17 composition of regional groundwater was stable throughout the growing season, with
18 mean $\delta^{18}\text{O}$ of -9.7 ± 0.07 (‰). Stream water is tightly linked with groundwater in this
19 region, and $\delta^{18}\text{O}$ values of stream water (data not shown) were generally related to those
20 of floodplain groundwater; therefore, stream water was not treated as a separate source.

21 $\delta^{18}\text{O}$ of tree xylem water

23 *Salix gooddingii*

Salix (willow) exhibited little variation in water-source use over the growing season among the three sites and relied predominantly on groundwater (Fig. 1). $\delta^{18}\text{O}$ values of this species were not significantly enriched above those of groundwater at any site or any sampling period ($p > 0.13$). $\delta^{18}\text{O}$ values of *Salix* were not different among sites or sampling periods ($p > 0.07$), and this species did not appear to use significant amounts of precipitation at any site, even in August after a significant precipitation event. Although $\delta^{18}\text{O}$ values of *Salix* increased at the intermittent and ephemeral stream sites in August, these shifts mirrored changes in groundwater $\delta^{18}\text{O}$ within the floodplain.

Populus fremontii

$\delta^{18}\text{O}$ values of xylem water in *Populus* (cottonwood) varied seasonally and apparently responded to monsoon precipitation events (Fig. 1). *Populus* relied on groundwater during the rainless period in June and July, but showed evidence of water use from shallow soil during the rainy season. The $\delta^{18}\text{O}$ values of *Populus* did not differ from that of floodplain groundwater in June and July at any of the three sites ($p > 0.19$). However, use of water from shallow soil layers during the summer rainy period (August) developed differently among the three riparian habitats studied. These habitat-related differences in $\delta^{18}\text{O}$ of *Populus* were reflected statistically in a significant interaction between sampling date and site ($p = 0.05$). Specifically, the difference between $\delta^{18}\text{O}$ of *Populus* and that of floodplain groundwater varied between all sites in August ($p < 0.0025$). $\delta^{18}\text{O}$ values of *Populus* were 0.4 ‰ more positive than that of floodplain groundwater at the perennial stream site ($p = 0.01$), and showed the greatest difference (+2.1‰) above floodplain groundwater at the ephemeral stream site ($p < 0.0001$).

1 However, $\delta^{18}\text{O}$ of *Populus* was more negative than that of floodplain groundwater at the
2 intermittent site (2-sided t-tests; $p < 0.03$).

3 4 *Prosopis velutina*

5 Similar to *Populus*, water sources of *Prosopis* (mesquite) varied seasonally in
6 response to monsoon rain events (Fig. 1). $\delta^{18}\text{O}$ values of *Prosopis* were affected by the
7 interaction between site and sampling date ($p = 0.04$). During the dry season (June and
8 July), mean $\delta^{18}\text{O}$ of *Prosopis* was similar to floodplain groundwater ($p > 0.12$) except at
9 the ephemeral stream site in July ($p = 0.04$). *Prosopis* $\delta^{18}\text{O}$ values were enriched relative
10 to floodplain groundwater in August at the intermittent and ephemeral site ($p < 0.02$)
11 indicating use of monsoon-derived shallow soil water. *Prosopis* $\delta^{18}\text{O}$ did not differ from
12 floodplain groundwater at the perennial stream site in August ($p = 0.11$). However, there
13 was considerable variation among $\delta^{18}\text{O}$ values of individual trees at the perennial stream
14 site that indicated some trees used groundwater while others used a combination of
15 shallow soil water and groundwater. This was reflected in the difference between plant
16 $\delta^{18}\text{O}$ and groundwater $\delta^{18}\text{O}$. These data indicated that $\delta^{18}\text{O}$ values of *Prosopis* were
17 similarly enriched relative to floodplain groundwater in June and August at the
18 intermittent and perennial stream sites ($p > 0.11$). However, trees at the ephemeral site
19 were more enriched relative to groundwater than at the other two sites ($p < 0.01$).

20 21 δD - $\delta^{18}\text{O}$ plots

22 Isotope values of *Populus*, *Salix*, and *Prosopis* water in δD - $\delta^{18}\text{O}$ space plotted
23 near groundwater and soil water from 100-cm depth at the perennial stream site (Fig. 2).

At the intermittent stream site, values for *Populus* and *Salix* were between local floodplain groundwater (sampled in July and August) and water from the 100-cm depth, but *Prosopis* plotted between soil water from the 10-, 25- and 100-cm depths. *Salix* values were similar to those of groundwater at the ephemeral stream site and *Populus* values were between those of groundwater and 100-cm soil demonstrating potential use of shallow soil water. *Prosopis* plotted with soil water from the 25- and 100-cm at the ephemeral stream site.

$\delta^{18}\text{O}$ and gravimetric content of soil water

The large rainfall event in August caused gravimetric water content (θ_g) in the shallow soil layers to increase at all sites (Fig. 3). θ_g increased from 5% in June to 18% in August in the upper 10 cm at the perennial reach, whereas θ_g at this depth increased from 2% to 6% and from 2% to 8% at the ephemeral and intermittent stream sites, respectively. Changes in θ_g at the 25-, 50-, and 100-cm depths between June and August were minimal along the perennial and intermittent reaches. θ_g increased slightly over the same period at the 25- and 50-cm depths along the ephemeral reach. Soil water $\delta^{18}\text{O}$ values were more positive in upper than in lower layers (Fig. 3), and became more negative with depth. $\delta^{18}\text{O}$ values at 100 cm (-8.0‰) were similar to those of groundwater at the perennial site, however $\delta^{18}\text{O}$ values at the same depth were approximately -6.0‰ at the ephemeral and intermittent reaches. $\delta^{18}\text{O}$ values of soil water in the upper 25 cm of soil resembled $\delta^{18}\text{O}$ of summer monsoon rainfall (Fig. 1).

Fraction of transpiration water derived from shallow soil

1 $\delta^{18}\text{O}$ of *Salix* did not differ from groundwater at any period and therefore the
2 fraction of water derived from shallow unsaturated soil layers was assumed to be zero.
3 When $\delta^{18}\text{O}$ of *Prosopis* and *Populus* differed from groundwater at the perennial and
4 ephemeral stream sites, the percentage of shallow (0-50 cm) soil water use was calculated
5 from the 2-compartment mixing model (Eqn. 1 and Table 2). Initially, the percentage of
6 transpiration water derived from shallow soil was calculated using $\delta^{18}\text{O}$ of floodplain
7 groundwater. However, trees at all sites appeared to have access to a source of water that
8 was more negative in $\delta^{18}\text{O}$ than local floodplain groundwater, such as regional
9 groundwater. This produced negative values for soil water use for three trees, which
10 were set to zero. Therefore, the average of local floodplain groundwater and regional
11 groundwater $\delta^{18}\text{O}$ was used for comparison, which may overstate the percentage of soil
12 water used by *Populus* and *Prosopis*. The average difference between the two models
13 was 7%.

14 In August after a summer rainfall event, *Populus* derived 8 to 16% of its
15 transpiration from shallow soil layers at the perennial stream site and between 26 to 33%
16 from soil water at the ephemeral stream site (Table 2). The proportion of *Populus*
17 transpiration water from shallow soil layers at the perennial site was significantly less
18 than that at the ephemeral stream site ($p < 0.03$). After the August rain event, shallow
19 soil water comprised 53 to 57% of transpiration water of *Prosopis* at the ephemeral
20 stream site. (Table 2). *Prosopis* was not different from groundwater ($p = 0.11$) at the
21 perennial site therefore mixing was assumed to be zero. In July at the ephemeral stream
22 site, $\delta^{18}\text{O}$ of *Prosopis* was significantly enriched relative to floodplain groundwater, but

1 since shallow soil water content was low ($< 2\%$) at this time, this source was unlikely to
2 have contributed to plant transpiration.

3 The fraction of transpiration water derived from shallow soil layers was
4 calculated with the 3-compartment mixing model [Eqn. 2-4] at the intermittent site.
5 Groundwater $\delta^{18}\text{O}$ at this site changed substantially in August from prior periods (Fig.1),
6 yet many trees in August had $\delta^{18}\text{O}$ values comparable to floodplain groundwater sampled
7 in June and July. It appears that the August runoff moving through the stream channel
8 flowed laterally through the gravelly substrate at this site, creating a saturated zone of
9 water that was perched above the floodplain groundwater and had more positive $\delta^{18}\text{O}$
10 values than the underlying aquifer. Therefore, $\delta^{18}\text{O}$ values from three sources were used
11 in the model: shallow soil water in August; groundwater sampled in August; and
12 floodplain groundwater sampled in July. If $\delta^{18}\text{O}$ of a species differed significantly from
13 $\delta^{18}\text{O}$ of groundwater sampled in August then the 3-compartment mixing model was
14 applied. $\delta^{18}\text{O}$ of *Prosopis* was enriched relative to August groundwater ($p=0.02$).
15 However, $\delta^{18}\text{O}$ of *Populus* was more negative than August groundwater ($p = 0.03$). $\delta^{18}\text{O}$
16 of *Salix* did not differ from August groundwater, and therefore shallow soil water use was
17 assumed to be zero. *Prosopis* used 67% of the perched August groundwater, 30%
18 shallow soil water, and 2% of the deeper floodplain groundwater (Table 3). *Populus*
19 *fremontii* used -5% of the perched August groundwater, 9% shallow soil water, and 97%
20 of the deeper floodplain groundwater (Table 3). Negative percentages are an artifact
21 produced by inherent matrix sensitivity. The 3-compartment mixing model had high
22 matrix sensitivity, which produced large standard errors (Table 3). This was likely due to
23 the limited variation in the isotopic composition of water sources. To synthesize 2- and

3-compartment model results and provide a conceptual interpretation of root function in this system, the fraction of transpiration water derived from shallow soil water was plotted in relation to groundwater depth (Fig. 4).

Predawn water potential

Predawn water potentials (Ψ_{pd}) in *Salix* and *Populus* were high (between -0.75 and -0.25 MPa) and changed little over the growing season (Fig. 5). These two species apparently had access to groundwater even at the ephemeral stream site where groundwater depth averaged 4 m. In June, when stream flow was still present and groundwater tables were less than 3 m deep at the intermittent site (Table 1), the effect of site ($p < 0.045$) on Ψ_{pd} was consistent across all species. During June, Ψ_{pd} values did not differ between the perennial and intermittent reaches ($p > 0.12$) and trees at these sites exhibited higher water potentials relative to those at the ephemeral stream site ($p < 0.02$). Ψ_{pd} of *Salix* and *Populus* did not vary between sites in July ($p > 0.10$). In August, *Salix* and *Populus* Ψ_{pd} values were similar at the ephemeral and perennial reaches ($p > 0.73$), but both species exhibited slightly higher water potentials along the intermittent reach compared to those measured at the other two sites ($p < 0.05$). Ψ_{pd} of *Prosopis* showed considerable seasonal variation (Fig. 5). The lowest Ψ_{pd} values (between -1 to -1.75 MPa) were observed in July just before the onset of the summer rainy period. The lowest Ψ_{pd} values in *Prosopis* during the dry season were observed at the intermittent stream site, but did not differ significantly from those at the ephemeral site ($p = 0.27$). In July, *Prosopis* along these reaches had lower water potentials than at the perennial reach ($p = 0.0005$).

The relationship between Ψ_{pd} and $\delta^{18}O$ of xylem water during the growing season was evaluated for trees at the perennial and ephemeral stream sites. Mean values at each sampling period are shown (Fig.6), however regression analyses were based on all observations. There were no significant relationships between these variables at either of the two sites in *Salix* ($p > 0.09$). Ψ_{pd} and $\delta^{18}O$ likewise were not correlated in *Populus* and *Prosopis* at the perennial stream site. However, at the ephemeral stream site, seasonal changes in water source availability that produced enriched $\delta^{18}O$ values of plant were accompanied by less negative Ψ_{pd} values for both *Populus* ($p = 0.0091$; $\Psi_{pd} = -0.14 + 0.04 \delta^{18}O$, $r^2 = 0.15$) and *Prosopis* ($p = 0.0007$; $\Psi_{pd} = 0.02 + 0.17 \delta^{18}O$, $r^2 = 0.43$).

4. Discussion

Reed (1988) classified these dominant species of low-elevation riparian ecosystems in southern Arizona as obligate wetland (*Salix gooddingii*), facultative wetland (*Populus fremontii*) and facultative upland (*Prosopis velutina*) based on their probability of occurrence within the heterogeneous floodplain environment. This study provides new insight into belowground responses of these species across sites with very different patterns of groundwater availability and within a climatic region that receives a substantial input of precipitation late in the growing season from the regional monsoon. Within this setting, substantial variation among species and populations was found for fractional use of soil water derived from these late summer storms. Sites where groundwater was deep and stream flow duration was intermittent or ephemeral promoted greater fractional use of soil water by *Populus* and *Prosopis*, but not *Salix*. This study, as

1 well as others (Dawson and Ehleringer 1991, Smith *et al.* 1991, Busch *et al.* 1992,
2 Mensforth *et al.*, 1994, Thorburn and Walker 1994, Dawson and Pate 1996, Jolly and
3 Walker 1996, Kolb *et al.* 1997), confirms that ‘phreatophytes’ encompass a wide
4 spectrum of functional types that respond uniquely to spatial and temporal variation in
5 the distribution of available water in the rhizosphere.

6 *Salix gooddingii* appeared to be most critically tied to groundwater among the
7 three species examined at our sites within the San Pedro River drainage system. Predawn
8 leaf water potentials in this species were high and did not change in response to seasonal
9 inputs of precipitation, and isotopic composition of xylem water mirrored that of
10 groundwater in the local floodplain aquifer. *Salix* apparently used water only from the
11 saturated zone or capillary fringe above the water table (Figs.1 and2), and therefore did
12 not respond to precipitation, even at the ephemeral stream site where groundwater depth
13 was greater than 4 m. *Salix* apparently develops roots for water uptake only in the
14 capillary fringe or saturated zone in these alluvial soils.

15 *Populus fremontii* and *Prosopis velutina* exhibited greater flexibility for use of
16 precipitation than did *Salix* along the San Pedro River. Use of monsoon precipitation
17 may have reduced water stress as evidenced by the relationship between Ψ_{pd} and $\delta^{18}O$ in
18 these species at the ephemeral stream site (Fig. 6). Greater depth to groundwater was
19 associated with greater fractional use of soil water during the monsoon season for these
20 species (Fig. 4). Thus, groundwater depth may be a good predictor of fractional water
21 source use in this ecosystem. *Prosopis* exhibited a linear response in the proportion of
22 soil water used for transpiration along a gradient of greater depth to groundwater. The
23 response of *Populus* indicated that this species used shallow soil water at all sites, but

1 used a greater proportion of soil water at the ephemeral stream reach when depth to
2 groundwater exceeded 4 m. *Populus* potentially exhibits a threshold response in contrast
3 to the linear response observed in *Prosopis*. In contrast, Busch *et al.* (1992) observed no
4 shallow soil water use by *Populus* on the Lower Colorado and Bill Williams Rivers in
5 western Arizona. Our sites in southeastern Arizona receive summer precipitation inputs
6 substantially greater than in the arid Mojave desert, where Busch *et al.* conducted their
7 study. Leaffler and Evans (1999) found that adult *Populus* along the Rio Grande River
8 floodplain in central New Mexico responded photosynthetically to growing season
9 precipitation in years when stream flow along the river was low, but not when stream
10 flow was high. Temporal variation for precipitation use in *Populus* observed in the Rio
11 Grande study apparently was similar to the spatial variation that was observed along the
12 San Pedro River.

13 *Prosopis velutina* exhibited substantial use of soil water during the summer rainy
14 period at the intermittent and ephemeral stream sites (fig. 4). δD - $\delta^{18}O$ plots (Fig. 2) from
15 ephemeral and intermittent stream reaches indicated that soil water from the 10-, 25- and
16 100-cm depths were important sources of transpiration water for this species. Along the
17 perennial reach the amount of shallow soil water use was assumed to be zero because
18 $\delta^{18}O$ was not different than that of floodplain groundwater (Fig. 4). This was likely due
19 to the high variability in $\delta^{18}O$ values of *Prosopis* at this site, which indicated that some
20 individual trees were using shallow soil water (up to 54%), while several trees relied
21 solely on groundwater. *Prosopis* apparently is highly flexible in its use of various water
22 sources. *Prosopis* predawn water potentials (Fig. 5) declined abruptly in July when water
23 table levels dropped and stream flow ceased at the intermittent site (see also Stromberg *et*

1 *al.* 1993). However, monsoon rains quickly ameliorated water stress in this species at all
2 sites. These data suggest that *Prosopis* may not develop extensive roots into saturated
3 zones within the soil profile and likely uses water from the capillary fringe.

4 The amount of summer rainfall in southeastern Arizona is enough to promote soil
5 water use in *Populus fremontii*. While the proportion of soil water use was higher at sites
6 with greater depth to groundwater, isotopic data do not indicate whether the *amount* of
7 soil water extracted by these trees differed between sites. This is an important distinction
8 because the amount of water gained from a soil compartment by root systems illustrates
9 the potential constraints and allocation tradeoffs that may explain root system dynamics
10 in these heterogeneous environments. The amount of water moving through *Populus*
11 trees from shallow soil layers was calculated by multiplying the fraction of xylem water
12 from this source and maximum sap flux in August at the perennial and ephemeral stream
13 sites. Sap flux data were obtained from Schaeffer and Williams (*this issue*) using the
14 same trees that were sampled for water sources. Three trees of similar size (0.5 –0.8 m
15 stem diameter) were selected at each site to minimize tree size effects. The total amount
16 of transpiration flux derived from soil water based on this calculation was 2.8 and 10.5 g
17 cm⁻² sapwood area hr⁻¹ at the perennial and ephemeral stream sites, respectively. Based
18 on this simple calculation, nearly four times as much water moving through the sapwood
19 of *Populus* trees was coming from shallow soil at the ephemeral stream site compared to
20 that at the perennial stream site. However, maximum sap flux was approximately the
21 same at the perennial and ephemeral stream reaches (35.0 and 40.7 g cm⁻² day⁻¹,
22 respectively). Total daily transpiration was compared by selecting days with similar solar
23 radiation and vapor pressure deficit. Total transpiration flux was 415.9 and 458.9 g cm⁻²

1 day⁻¹ at the perennial at ephemeral stream sites, respectively. Hence, 382.7 and 338.9 g
2 cm⁻² day⁻¹ was derived from groundwater, and 33.2 and 119.1 g cm⁻² day⁻¹ were derived
3 from shallow soil water at the perennial and ephemeral reach respectively. Total water
4 use was similar, but the amount of water from shallow soil layers was greater, while the
5 amount from groundwater was less at the ephemeral reach relative to the perennial reach.
6 Root excavation studies of *Populus* trees along the Mojave River in southern California
7 (G. C. Lines, *pers. comm.*) revealed a greater percentage (between 10-50%) of roots in
8 the upper meter of soil at sites where groundwater levels were more than 3 m in depth,
9 compared to sites where groundwater was only 1.5 m deep. Taken together, these data
10 suggest that there may be allocation tradeoffs associated with deploying roots in a
11 particular soil layer. Exploitation of groundwater may come at the expense of water use
12 from other sources, or, alternatively, when groundwater becomes deep or unreliable, trees
13 may develop more shallow roots to exploit other water sources.

14 Declining groundwater in the San Pedro River system will have a strong negative
15 impact on the survival of *Salix*, because water sources appear to be limited to
16 groundwater. If mature *Populus* is able to continue deep root growth during groundwater
17 recession by augmenting transpiration needs with precipitation taken up by shallow
18 lateral roots, this species may be able to tolerate some recession of groundwater depth.
19 However, it appears that *Populus* must keep roots in the saturated zone to maintain high
20 predawn water potentials. Therefore, persistent long-term declines in groundwater levels
21 will likely limit this species as well (*see also* Stromberg *et al.* 1996). *Prosopis* is highly
22 flexible in its use of water sources and is likely to become more dominant in the riparian
23 landscape if declining groundwater levels persist. However, *Prosopis* tree growth may be

1 limited in stature relative to historic riparian mesquite woodlands if groundwater is
2 limited (Stromberg *et al.* 1993, Stromberg 1993b).

3 In conclusion, some riparian trees, even those commonly associated with shallow
4 groundwater, can use substantial amounts of precipitation to meet transpiration
5 requirements. One of the main goals of the SALSA program is to estimate and model
6 transfer of groundwater *via* riparian evapotranspiration on a basin-wide scale (*see*
7 Goodrich *et al.*, *this issue*). These data suggest that species composition in riparian
8 forests (abundances of *Salix*, *Populus*, and *Prosopis*) together with habitat conditions
9 (depth to groundwater) will interactively determine the fraction of transpiration derived
10 from groundwater at the stand level. Integrated over a large area, the contribution of soil
11 water to transpiration in these forests can be substantial, yet easily misrepresented in
12 scaling algorithms. Results of this study indicate that water balance calculations in
13 riparian forests from semi-arid regions should take into consideration species-
14 environment responses within the heterogeneous floodplain ecosystem.

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Table 1. Depth to groundwater (m) from the ground surface at the three study sites along the San Pedro River, Arizona in 1997. Data were obtained from a single well that penetrated the local floodplain groundwater at the perennial and intermittent site. Data at the ephemeral study site are an average of 2 wells. All wells were located within 10 meters of the stream channel.

Month	Perennial	Intermittent	Ephemeral
Feb.	--	2.28	3.86
Mar.	0.95	2.27	3.90
Apr.	1.98	--	4.21
June	1.42	2.61	4.43
July	2.43	3.32	4.69
Aug.	2.08	2.67	4.48
Sept.	1.91	2.53	4.31
Average	1.8	2.61	4.26

Table 2. Percentage of xylem water (± 1 SE) derived from shallow soil layers in August after a monsoon rain event. Percent shallow soil water was calculated with a 2-compartment mixing model (Eqn. 1). Normal type indicates the percent of water derived from shallow soil layers with local floodplain groundwater as an end member of the model. **Bold face** type indicates an estimate based on an average of regional groundwater and local floodplain water. Different letters indicate significant differences between the ephemeral tributary and the perennial reach of the San Pedro River, Arizona.

Species	Perennial Stream Site			Ephemeral Stream Site		
	June	July	August	June	July	August
<i>Salix gooddingii</i>	0	0	0	0	0	0
<i>Populus fremontii</i>	0	0	8 ± 8 A	0	0	26 ± 7 B
			16 ± 2 A			33 ± 7 B
<i>Prosopis velutina</i>	0	0		0	0	52 ± 5
						57 ± 7

Table 3. Percentage of xylem water (± 1 SE) derived from shallow soil layers in August after a monsoon rain event for trees along an intermittent reach of the San Pedro River, Arizona. Percent soil water was calculated with a 3-compartment linear mixing model [Eqn. 3] for species whose mean $\delta^{18}\text{O}$ values were significantly different than that of groundwater ($p < 0.05$).

Species	Intermittent Stream Reach		
	% shallow soil water	% deep groundwater	% shallow groundwater
<i>Populus fremontii</i>	9 ± 4	97 ± 16	-5 ± 13
<i>Prosopis velutina</i>	30 ± 14	3 ± 27	67 ± 40

Figure Captions

Figure 1. Mean $\delta^{18}\text{O}$ values of *Salix goodingii*, *Populus fremontii*, and *Prosopis velutina*, regional groundwater, floodplain groundwater, and precipitation during the 1997 growing season along perennial, intermittent and ephemeral reaches of the San Pedro River in southeastern Arizona. Vertical bars represent ± 1 SE of the mean.

Figure 2. $\delta\text{D} - \delta^{18}\text{O}$ values from trees, soil, groundwater, and rainfall in August 1997 along perennial and intermittent reaches and an ephemeral tributary of the San Pedro River in southeastern Arizona. Fitted line is the global meteoric water line (GMWL) ($\delta\text{D} = 8.31 * \delta^{18}\text{O} + 10.8$) (Clark and Fritz 1998). Soil water was extracted from 10-, 25-, and 100- cm depths.

Figure 3. Gravimetric soil water content (θ_g) and soil water $\delta^{18}\text{O}$ at 5-, 10-, 25-, 50-, and 100-cm depths in June prior to the onset of the summer ‘monsoon’ rainy season, and August after a large precipitation event. The arrows on $\delta^{18}\text{O}$ plots indicate the $\delta^{18}\text{O}$ values of local floodplain groundwater in June (*open arrow*) and August (*closed arrow*). Soils were sampled in 1997 along a perennial, intermittent and ephemeral reach of the San Pedro River in southeastern, Arizona. Horizontal bars represent 1 SE of the mean and are presented when possible with the exception of soil $\delta^{18}\text{O}$ values sampled in June.

Figure 4. The relationship between depth to groundwater and the percentage of plant transpiration water derived from shallow soil water in August after a monsoon rain event for *Salix goodingii*, *Populus fremontii*, and *Prosopis velutina* sampled along the San Pedro River in Arizona.

Figure 5. Mean predawn leaf water potential (Ψ_{pd}) of *Salix gooddingii*, *Populus fremontii*, and *Prosopis velutina* along perennial and intermittent reaches, and an ephemeral tributary of the San Pedro River in southeastern Arizona in 1997. Horizontal bars represent 1 SE of the mean.

Figure 6. Relationship between mean $\delta^{18}\text{O}$ and mean predawn leaf water potential (Ψ_{pd}) at each sampling period over the 1997 growing season for *Salix gooddingii*, *Populus fremontii*, and *Prosopis velutina* at a perennial reach and an ephemeral tributary of the San Pedro River in southeastern Arizona. Horizontal and vertical bars represent ± 1 SE of the mean. Fitted lines are the statistically significant regression relationships for a given species ($\alpha = 0.05$).